

Rhigonematida (Nematoda)
of *Rhinocricus bernardinensis*
(Rhinocricidae; Spirobolida; Diplopoda)
with comments on r- and K-selection in
nematode parasites of diplopods

by

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With 11 figures

ABSTRACT

Six rhigonematids (Rhigonematida; Nematoda) including five new species are described from *Rhinocricus bernardinensis* (Rhinocricidae; Spirobolida; Diplopoda) collected from the region of the Iguassu Falls during an expedition to Paraguay. *Heth chunyi* n. sp., most similar to *H. spinosum*, is distinguished on the basis of differences in cervical cuticular ornamentation of the female and in having a longer spicule with a bifid distal extremity. *Heth parartigasi* n. sp. and *H. magnavulvaris* n. sp. are most similar to *H. artigasi* but differ in vulvar morphology: In *H. parartigasi* the vulva is non-salient and there is a prevulvar area rugosa; in *H. artigasi* and *H. magnavulvaris* there is no area rugosa and the vulva is salient; in *H. artigasi*, the anterior lip of the vulva overhangs the posterior lip only slightly whereas in *H. magnavulvaris* it forms a prominent fleshy lobe. Males corresponding to *H. parartigasi* or *H. magnavulvaris* are described as *Heth* sp. and differ from those of *H. artigasi* in having a longer gubernaculum and spicule and in that the distal extremity of the latter is bifid. *Ransomnema paraguayense* n. sp. most resembles *R. christiei* but differs in disposition of caudal papillae and in having a longer right spicule. *Carnoya mackintoshae* n. sp. most resembles *C. dollfusi* but females of the species differ slightly in cervical cuticular ornamentation, in that the cephalic papillae are subterminal in the new species and terminal in *C. dollfusi*, in the absence of teeth at the base of the buccal capsule of

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C. mackintoshae and in vulvar morphology; males differ slightly in spicular morphology. *Rhigonema subulata* (Artigas, 1926) is redescribed.

The nematode fauna in the posterior gut of diplopods differs from other examples where several parasite species occur in the same host organ in that it consists of three superfamilies (Thelastomatoidea, Rhigonematoidea and Ransomnematodea) rather than a single lineage. It is suggested that the Rhigonematoidea are relatively K-selected whereas the Thelastomatoidea and Ransomnematodea are more r-selected.

INTRODUCTION

During a zoological expedition of the Geneva Museum of Natural History to Paraguay in 1982¹, two specimens of *Rhinocriscus bernardinensis* were collected. These were found to be infected with seven nematode species, all occurring in the posterior intestine. One species, *Thelastoma dessetae* Adamson, 1985 was described in a previous communication (ADAMSON 1985); the present article describes the remaining six species, five of which are new.

Several authors (CHABAUD 1956; DURETTE-DESSET 1971; INGLIS 1965, 1971; CHABAUD & DURETTE-DESSET 1978) have discussed problems raised by the coexistence of several nematode species parasitizing the same host organ. This phenomenon brings up two major questions: how did such species flocks arise? How do the species coexist? None of these authors referred to the nematode fauna of diplopods. However, this fauna is particularly diverse and appears to include species with differing life history tactics. In this article, therefore, in addition to describing the species, I compare the diplopod fauna with other nematode species flocks and examine the life-history tactics of the component species in terms of r- and K-selection.

MATERIALS AND METHODS

Diplopods, collected in the region of the Iguassu Falls were broken in half and fixed in 70% ethanol immediately after capture; identifications were made by Dr. J. P. Mauries and Professor J. M. Demange of the Laboratoire des Arthropodes, Muséum national d'Histoire naturelle, Paris (MNHN).

Nematodes collected from the posterior intestine were stored in 70% ethanol before being cleared and studied in lactophenol. Type and other specimens are stored in the Laboratoire de Zoologie (Vers), MNHN: KP 159 and KP 160, and the Geneva Museum of Natural History (MHNG 982.1727-1732).

DESCRIPTION OF SPECIES

Heth clunyi n. sp.

Material Examined: Three males (including holotype) and two females were recovered from KP 159 and one male was recovered from KP 160 (also MHNG 982.1727).

DESCRIPTION (Figs 1 and 2)

¹ Expedition carried out in collaboration with 'la coopération technique Suisse' and the 'Inventario biológico du Ministerio de Agricultura y Ganadería, Paraguay'.

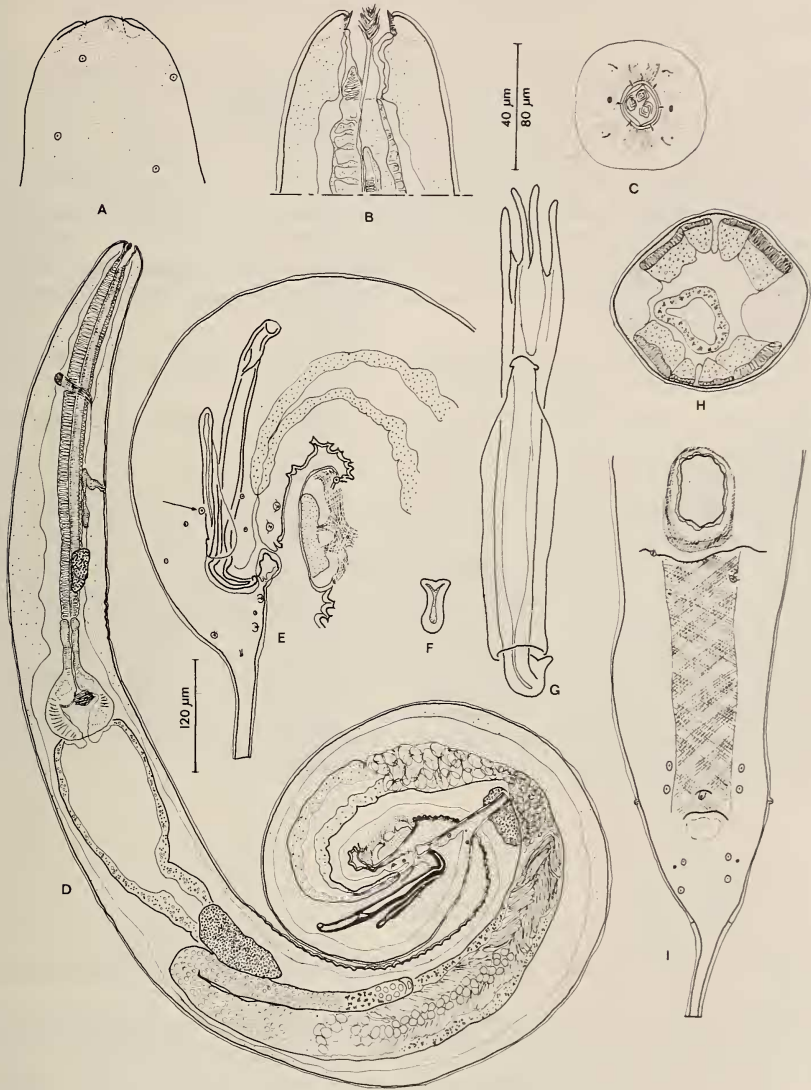


FIG. 1.

Heth clunyi n. sp., male. A and B, lateral views of cephalic extremity, superficial view and optical section. C, superficial apical view. D, entire worm, lateral view. E, caudal extremity, lateral view. Note small somatic papillae; arrow points to lateral adanal papilla. F, distal extremity of spicule. G, spicule and gubernaculum in dorsal view. H, transverse section through body. I, caudal extremity, ventral view.

(A, B, C, F, G = 40 μ m scale; D = 120 μ m scale; E, H, I = 80 μ m scale)

General: Relatively large *Heth* with broad cephalic extremities. Body cuticle with faint striations 2 to 3 μm apart, these becoming indistinct in anal region. Somatic papillae numerous.

Male: Oral opening oval surrounded by outer circle of four submedian pairs of inconspicuous nerve endings (presumably representing outer labial and cephalic papillae) and two amphids, and inner circle of six small inner labial papillae.

Buccal cavity broad and urceolate. One dorsal and two subventral prominent pennate projections extending from base of buccal capsule to near edge of oral opening.

Ventral sucker prominent. Fifteen caudal papillae, distinguished from somatic papillae by larger size: one pair subventral just posterior to ventral sucker; two pairs subventral just anterior to anus and one median unpaired on anterior anal lip; one pair small lateral adanal; two pairs subventral and one pair subdorsal postanal. Phasmids just posterior to last pair of caudal papillae.

Spicule well-cuticularized, its distal end forming prominent hook with bifid extremity. Gubernaculum well-developed.

Female: Buccal cavity with one dorsal and two subventral lappet-like cuticular projections.

Cephalic and cervical cuticular ornamentation as follows (from anterior to posterior): eight submedian, posteriorly-directed spines (four subdorsal and four subventral) on posterior border of oral opening; two subdorsal and two subventral pairs of comb-like formations: anterior pairs with 11 to 13 spines and posterior pairs with 8 to 10; approximately 15 transverse rows of tiny spines behind last pair of comb-like formations on dorsal and ventral sides; cervical collar with 53 to 67 posteriorly-directed spines of similar size and, on each side, two much larger spines; two lateral pairs of long posteriorly-directed spines arranged *in tandem* posterior to cervical collar; many small button-like formations, each with 2 to 8 posteriorly-directed spines and central nerve ending, arranged in four subdorsal and four subventral irregular longitudinal rows posterior to cervical collar, becoming smaller and gradually giving way to somatic papillae posteriorly.

DIMENSIONS

Male (mean and standard deviation of four specimens of which holotype in parentheses).

Length 2.62 ± 0.17 mm. Maximum width 169 ± 32 μm near midbody. Buccal cavity 29 ± 2 μm long. Oesophagus 561 ± 59 μm long consisting of corpus 430 ± 56 μm and isthmus 56 ± 1 μm long, and bulb 76 ± 4 μm long and 80 ± 6 μm wide. Nerve ring 177 ± 14 μm , excretory pore 292 ± 21 μm and flexure of testis 828 ± 64 μm from anterior extremity. Ventral sucker 72 ± 8 μm long, 346 ± 57 μm from anus. Spicule 180 ± 12 μm , gubernaculum 89 ± 3 μm and tail 477 ± 44 μm long.

Female (2 specimens). — Length 3.09 (2.96) mm. Maximum width 214 (130) μm near midbody. Buccal cavity consisting of anterior portion 46 (42) μm and posterior striated portion 44 (35) μm long. Oesophageal corpus 262 (240) μm and isthmus 59 (47) μm long, and bulb 88 (99) μm long and 97 (110) μm wide. Nerve ring 173 (151) μm , excretory pore 225 (210) μm and vulva 2.18 (1.99) mm from anterior extremity. Tail 643 (721) μm long. Eggs 81-103 μm wide and 185-218 μm long.

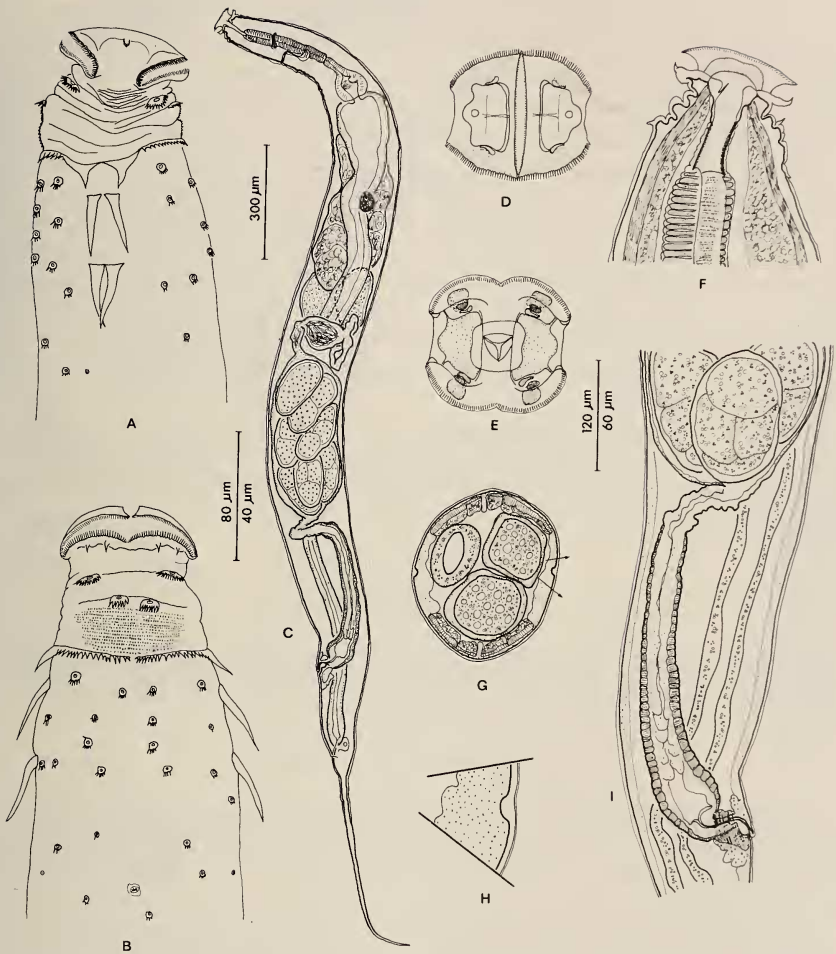


FIG. 2.

Heth clunyi n. sp., female. A and B, anterior extremity in superficial lateral and ventral views. C, entire worm, lateral view. D, superficial apical view. E, optical section through base of pseudolabia, apical view. F, cephalic extremity, optical section in lateral view. G, transverse section through body. H, detail of inset indicated in G. I, vulva and vagina, lateral view.

(A, B, F = 80 μm scale; C = 300 μm scale; D, E = 60 μm scale;
G, I = 120 μm scale; H = 40 μm scale)

DISCUSSION

Cephalic and cervical cuticular ornamentation in females of this species resembles that of *H. duvidosum* Artigas, 1929, *H. spinosum* Artigas, 1929, *H. perarmatum* Dollfus, 1952, *H. bifidispiculum* Adamson, 1982 and *H. mauriesi* Adamson, 1982: there are two pairs of comb-like formations ventrally and dorsally; the cervical collar is continuous or nearly continuous with two prominent lateral spine pairs; two pairs of long posteriorly-directed spines are arranged posterior to and *in tandem* with the lateral spines of the cervical collar and a variable number of button-like formations are present between these.

Heth clunyi is distinguished from all but *H. spinosum* and *H. perarmatum* by the fact that the cervical collar is interrupted briefly dorsally and ventrally. Although ARTIGAS (1929) did not refer to such an interruption in his original description of *H. spinosum*, I observed it in material which agreed in all other respects with his description (ADAMSON 1983), as well as in specimens of *H. perarmatum* placed in the Paris Museum (MNHN, Laboratoire de Zoologie, Vers: BD 8) by Dollfus. *Heth clunyi* differs from both of the above species by having fewer spines in the comb-like formations. This is most evident in the posterior pair where there are 8 to 10 as compared with 10 to 15 in *H. perarmatum* and 16 to 25 in *H. spinosum*.

Males of *H. clunyi* differ from those of *H. spinosum* in having a longer spicule (168 to 197 μm as compared with 130 to 140 μm) with a bifid distal extremity, and by the fact that the two subventral pairs of postanal papillae are closer to one another. Males of *H. perarmatum* are unknown.

Heth parartigasi n. sp.

Material Examined. — Eight females (including holotype) were recovered from KP 159 and two females were found in KP 160 (also MHNG 982.1728).

DESCRIPTION (Figs 3 and 4)

Cephalic extremity about as wide as long in apical view. Body cuticle with prominent transverse striations 1 to 2 μm apart becoming indistinct in anal region. One dorsal and two subventral lappet-like cuticular projections present in buccal cavity, each with tiny hairs on inner surface.

Cephalic and cervical cuticular ornamentation consisting of following (from anterior to posterior): two submedian pairs posteriorly-directed cuticular spines on dorsal and ventral sides just behind posterior edge of oral opening; in line with these in cervical region, two submedian pairs of posteriorly-directed cuticular hooks each with rootlet buried in body cuticle; on each side in cervical region, two long sublateral posteriorly-directed spines separated by lateral plate of smooth cuticle; on each side two sublateral spines near level of nerve ring.

Ovaries beginning near midbody region, running anteriorly and flexing posteriorly behind oesophagus before emptying into oviducts. Oviducts often containing egg surrounded by developing shell, fusing at spherical glandular chamber (seminal receptacle). Seminal receptacle connected to uterus by long duct lined by large glandular cells which apparently empty into lumen. Uterus, its upper region filled with spermatids, leading posteriorly to muscular vagina. Vulva just anterior to anus.

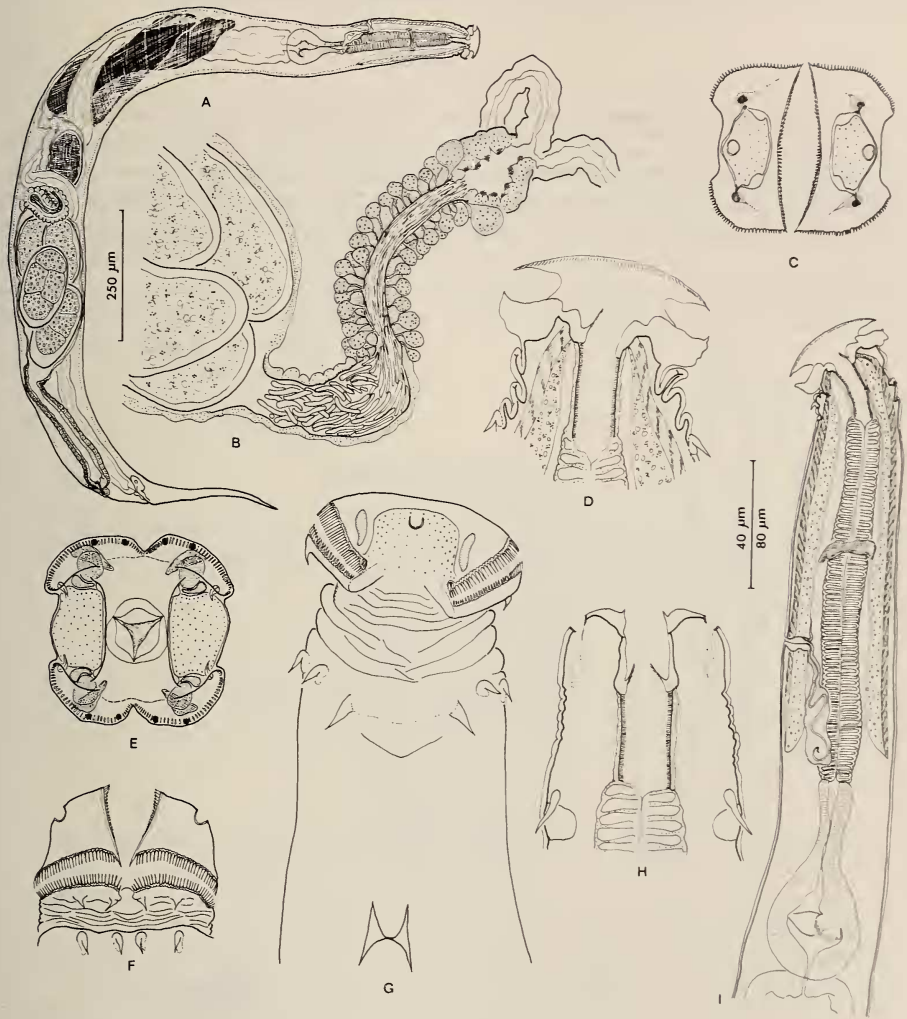


FIG. 3.

Heth parartigasi n. sp., female. A, entire worm, lateral view. B, junction of uterus and oviducts showing prominent gland cells and spermatids. C, superficial apical view. D, optical section through cephalic extremity. E, optical section through base of pseudolabia, apical view. F, cephalic extremity, superficial ventral view. G, cephalic extremity, superficial lateral view. H, optical section through cephalic extremity, ventral view. I, oesophageal region, lateral view.

(A = 250 μm scale; B to H = 40 μm scale; I = 80 μm scale)

Lateral fields extremely broad; lateral nerve giving off branches leading to small somatic papillae, these especially numerous just anterior to level of vulva. Cuticular striations anterior to vulva reinforced and forming *area rugosa*-like modification.

DIMENSIONS

(mean and standard deviation of 4 specimens of which holotype in parentheses)

Length 2.01 ± 0.14 (2.05) mm. Maximum width 179 ± 32 (194) μm near midbody. Buccal cavity with anterior portion 29 ± 3 (28) μm long and posterior striated portion 32 ± 3 (36) μm long. Corpus 221 ± 8 (226) μm and isthmus 43 ± 4 (39) μm long. Bulb

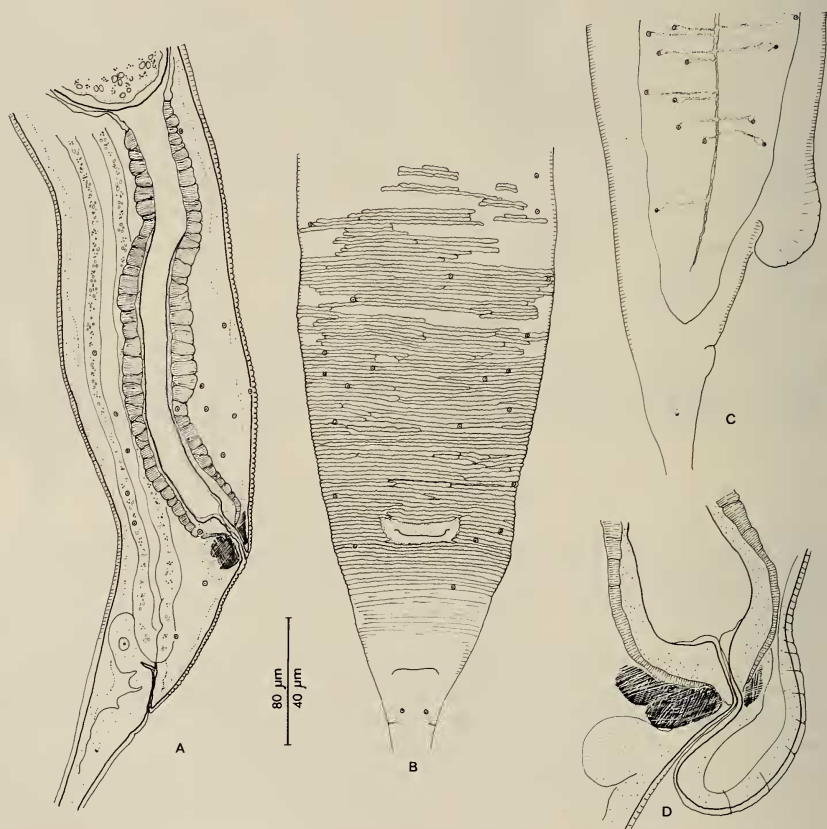


FIG. 4.

A and B, *Heth parartigasi* n. sp., female, vulva and anal region in lateral and ventral view.
C and D, *Heth magnavulvaris* n. sp.: C, vulva and anal region, lateral view;
D, detail of vulva, lateral view.

(A to C = 80 μm scale; D = 40 μm scale)

76 ± 4 (79) µm long and 75 ± 13 (88) µm wide. Nerve ring 142 ± 4 (146) µm, excretory pore 197 ± 7 (201) µm and vulva 1.67 ± 0.12 (1.71) mm from anterior extremity. Tail 251 ± 21 (261) µm long. Eggs 77 ± 9 µm wide 164 ± 18 µm long.

DISCUSSION

This and the following species are described on the basis of female morphology. Males corresponding to one or both species are described separately as *Heth* sp. (see below). *Heth parartigasi* n. sp. is very similar to *H. artigasi* Dollfus, 1952 in the form of the cervical and cephalic cuticular ornamentation. The type specimen of the latter species is in permanent mount (MNHN, Laboratoire des Vers: BD 8); it is excessively cleared and its structure is difficult to interpret. Nevertheless, the new species differs clearly from this material by its non-salient vulva and by the presence of an *area rugosa* anterior to the vulva. In addition, the last pairs of lateral cervical spines are broadly fused in *H. artigasi* and only slightly fused, if at all, in *H. parartigasi*.

Heth magnavulvaris n. sp.

Material Examined: Nineteen females (including holotype) were recovered from KP 159 and five females were recovered from KP 160 (also MHNG 982.1729).

DESCRIPTION (Fig. 4)

Identical to *H. parartigasi* except for the following:

- anterior lip of vulva forming broad swelling overhanging posterior lip;
- *area rugosa* absent.

DIMENSIONS

(mean and standard deviation of 5 specimens of which holotype in parentheses)

Length 1.97 ± 0.12 (2.07) mm. Maximum width 164 ± 13 (167) µm near midbody. Buccal capsule with anterior portion 25 ± 2 (24) µm long and posterior portion 30 ± 1 (29) µm long. Oesophageal corpus 203 ± 14 (199) µm and isthmus 46 ± 6 (56) µm long. Bulb 75 ± 6 (73) µm long and 68 ± 10 (61) µm wide. Nerve ring 131 ± 7 (120) µm, excretory pore 171 ± 17 (156) µm and vulva 1.64 ± 0.12 (1.75) mm from anterior extremity. Tail 250 ± 14 (249) µm long. Eggs 73 ± 7 µm wide and 161 ± 12 µm long.

DISCUSSION

As in *H. artigasi*, the vulva is salient in *H. magnavulvaris*. However the saliency is much more pronounced in the new species and is due to a highly swollen anterior vulvar lip. The extent of development of the vulvar lip does not appear to be related to age of worms since its prominence was similar in all specimens regardless of their size or of the number of eggs *in utero*. I therefore feel it is most prudent to describe the material as a new species distinct from *H. artigasi* and *H. parartigasi*.

Heth sp.

Material Examined: Twenty specimens were found in KP 159 and four specimens in KP 160.

DESCRIPTION (Fig. 5)

Relatively small worms bearing transverse striations 1 to 2 μm apart. Cephalic extremity and oral opening laterally compressed in apical view. Four submedian outer papillae present; inner papillae not observed. Amphids raised slightly.

Buccal cavity consisting of anterior portion rectangular in apical view its cuticular lining thickest posteriorly, and posterior portion subtriangular in apical view its cuticular lining with one dorsal and two subventral prominent striated thickening at its base. Pennate cuticular formations projecting anteriorly into buccal cavity from each thickening. Intestine not forming loop in body cavity.

Specimens examined highly contracted: spicule everted, caudal extremity curved sharply ventrally and ventral side of body with prominent fold of tissue between ventral sucker and anus. Longitudinal row of obliquely-oriented muscles running lateroventrally on either side of body beginning just anterior to ventral sucker and ending just anterior to anus. Extremities of muscles interweaving on ventral side.

Fifteen genital papillae present: one on either side of posterior border of ventral sucker; one on either side of body fold between ventral sucker and anus; one pair sublateral adanal; three pairs postanal of which two most anterior pairs subventral and located very close together on slight swelling, and third pair subdorsal on caudal appendage. Scattered somatic papillae, much smaller than genital papillae, also present.

Spicule slender, distally arcuate with bifid distal extremity. In four specimens spicule twisted slightly and its extremity directed laterally, from right to left in three specimens and from left to right in one. Gubernaculum with arcuate distal extremity abutting on postanal plate of thickened body cuticle.

DIMENSIONS

Length 1.54 ± 0.13 mm. Maximum width $97 + 17$ μm near midbody. Buccal cavity $24 + 2$ μm , oesophageal corpus $398 + 26$ μm and isthmus $49 + 3$ μm long. Bulb $61 + 6$ μm long and $57 + 8$ μm wide. Nerve ring $160 + 21$ μm and excretory pore $235 + 29$ μm from anterior extremity. Ventral sucker $39 + 6$ μm in diameter, $159 + 12$ μm anterior to anus. Spicule $97 + 6$ μm , gubernaculum $51 + 4$ μm and tail $116 + 10$ μm long.

DISCUSSION

This material doubtless corresponds to *H. parartigasi*, *H. magnavulvaris* or both (if the two species represent in fact a case of female polymorphism) since it has obvious affinities with male *H. artigasi* in the general shape of the cephalic extremity and disposition of the caudal papillae. The present material differs from *H. artigasi* in that the spicule and gubernaculum are longer and the distal extremity of the spicule is bifid. In addition, the plate of cuticle against which the gubernaculum rests is postanal in our material but intracloacal in *H. artigasi*. These differences support the proposal of the new species *H. parartigasi* and *H. magnavulvaris*.

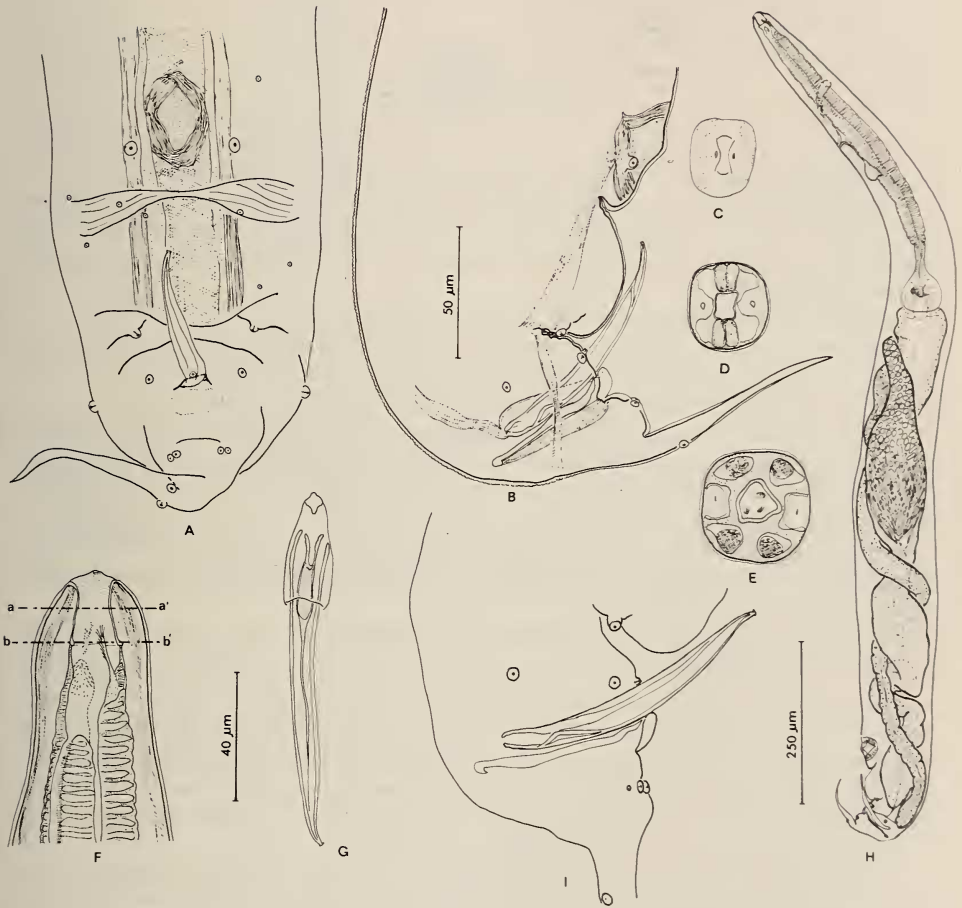


FIG. 5.

Heth sp., male. A and B, caudal extremity, ventral and lateral views. C to F, cephalic extremity; C, superficial apical view; D and E, optical sections taken at levels a/a' and b/b' respectively of lateral view F. G, spicule and gubernaculum, dorsal view. H, entire worm, lateral view. I, profile of caudal extremity of specimen with twisted spicule.

(A to G and I = 40 µm scale; H = 250 µm scale)

Ransomnema paraguayense n. sp.

Material Examined: One male (holotype), two females and one larva were recovered from KP 159 and two females and two larvae were found in KP 160 (also MHNG 982.1730).

DESCRIPTION (Figs 6 and 7)

General: Spindle-shaped worms with transverse striations about 2 μm apart beginning just posterior to cephalic extremity and continuing to near end of tail.

Oral opening triradiate, surrounded by two subdorsal and one ventral slightly developed lips. Tiny membranous cuticular extension projecting anteriorly from apex of each lip. Cephalic sense organs consisting of four inconspicuous outer papillae, six tiny inner papillae and two amphids.

Buccal cavity long and urceolate, composed of three parts:

(1) anterior portion in form of triangle with truncated apices in apical view and lined by thick layer of transparent cuticle apparently continuous with body cuticle;

(2) short middle portion surrounded by ring of sclerotized cuticle;

(3) long posterior portion with thick cuticular lining and bearing one dorsal and two subventral pennate cuticular projections each arising from small block of striated cuticle at base of buccal capsule; small cuticular hairs projecting from buccal capsule anterior to each pennate projection.

Four muscles present, running anteriorly along body wall and connecting to base of buccal capsule, two attached to dorsal block of striated cuticle and one to each subventral block.

Prominent dorsal and ventral commissures running around body between cuticle and hypodermis near level of midregion of oesophageal corpus and uniting in lateral fields.

Male: Testis, its blind end near midbody, extending anteriorly and flexing posteriorly 168 μm behind oesophageal bulb. Spermatocytes flattened and arranged in single file throughout much of testis, becoming subspherical to oblong in transformation zone; spermatids in seminal vesicle up to 75 μm long, slipper-shaped with central mass of chromatin. Epithelium of gonad between transformation zone and seminal receptacle containing many amber colored secretory vesicles. Vas deferens divided.

Ventral sucker consisting of inner portion about 35 μm in diameter roughly oval in ventral view and lying in muscular cup-like formation; cuticular surface of ventral sucker bearing 13 transverse rows of cuticular bosses, 14 to 18 bosses per row, each boss up to 3 μm high.

Three coelomocytes: one near flexure of testis and two located respectively 475 μm and 180 μm anterior to ventral sucker.

Fifteen caudal papillae present: two pairs lateroventral located about 74 μm anterior to anus; one pair lateroventral about 28 μm posterior to these; transverse row of three papillae on anterior anal lip; two pairs subventral papillae, on about 58 μm , the other about 100 μm posterior to anus; second pair slightly raised; two median papillae located respectively 135 μm and 164 μm posterior to anus. Phasmids near level of last papilla.

Swollen caudal alae present, beginning near level with third pair of pre-anal papillae and extending to near level of phasmids.

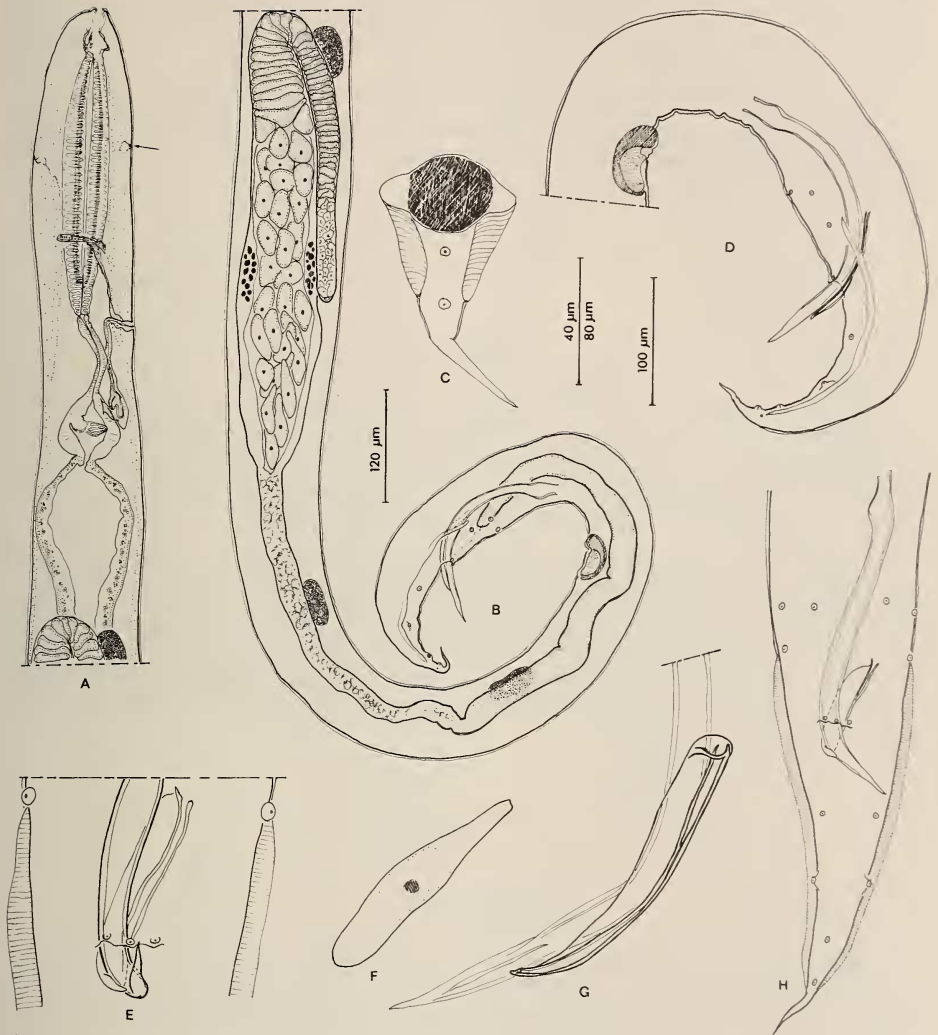


FIG. 6.

Ransonnema paraguayense n. sp., holotype male. A and B, anterior and posterior portions of worm, lateral view; note hemizonid (arrow in A). C, optical section through tail showing inflated caudal alae. D, caudal extremity, lateral view. E, anal region, ventral view showing left spicule and distal end of right spicule. F, spermatid from seminal vesicle. G, left spicule and distal end of right spicule, lateral view. H, caudal extremity, ventral view.

(A and B = 120 µm scale; C and E to G = 40 µm scale; D = 100 µm scale; H = 80 µm scale)

F e m a l e : Monodelphic, digonant. Ovaries pyriform emptying into oviducts with three prominent glandular cells near their midregions. One oviduct emptying into anterior, other into posterior end of uterus. Muscular vagina communicating with posterior end of uterus extending posteriorly to vulva. Eggs large with thin flexible shell containing embryos in early stage of development.

Two coelomocytes: one beside vagina, other about 175 μm posterior to vulva.

Slightly swollen inconspicuous caudal alae present, beginning near level of midregion of vagina and extending to just anterior to phasmids. Tail roughly conical with slight swelling at level of phasmids.

DIMENSIONS

M a l e holotype. — Length 2.28 mm. Maximum width 124 μm near midbody. Buccal capsule 48 μm , oesophageal corpus 276 μm and isthmus 91 μm long. Bulb 67 μm long and 65 μm wide. Nerve ring 247 μm and excretory pore 341 μm from anterior extremity. Terminal duct of excretory system 111 μm long. Ventral sucker 320 μm anterior to anus. Right spicule 263 μm , left spicule 106 μm and tail 192 μm long.

F e m a l e (allotype followed by paratype in parentheses). — Length 2.49 (2.73) mm. Maximum width 246 (238) μm near midbody. Buccal cavity 61 (70) μm , oesophageal corpus 333 (342) μm and isthmus 89 (92) μm long. Bulb 81 (77) μm long and 81 (77) μm wide. Nerve ring 317 (327) μm , excretory pore 404 (433) μm , anterior extremity of reproductive system 704 (764) μm and vulva 1.56 (1.73) mm from anterior extremity. Terminal duct of excretory system 93 (115) μm and tail 172 (188) μm long. Eggs 126-155 μm long and 72-95 μm wide (six eggs measured).

DISCUSSION

Ransomnema paraguayense is most similar to *R. christiei* Dollfus, 1952 (from *Rhinocricus cachoeirensis* from Sao Paulo State, Brazil): the left spicule is long (nearly 100 μm), the first two pairs of caudal papillae are located at about the same level, the vagina is directed nearly perpendicular to the body wall at the vulva and the terminal duct of the excretory system is long (over 90 μm).

The species differ in the following: in *R. christiei* the three most anterior pairs of caudal papillae are located within 15 μm of one another whereas in the new species the two most anterior pairs are over 20 μm from one another and almost 30 μm from the third pair; the anterior papilla pair is about 50 μm anterior to the anus in *R. christiei* but over 70 μm anterior to the anus in *R. paraguayense*; the first postanal papilla pair is about 25 μm from the anus in *R. christiei* and almost 60 μm postanal in the new species; the ventral sucker is further from the anus in the present material (320 μm as compared with 230 μm in *R. christiei*); the right spicule is longer in *R. paraguayense* (263 μm compared with 205-209 in *R. christiei*).

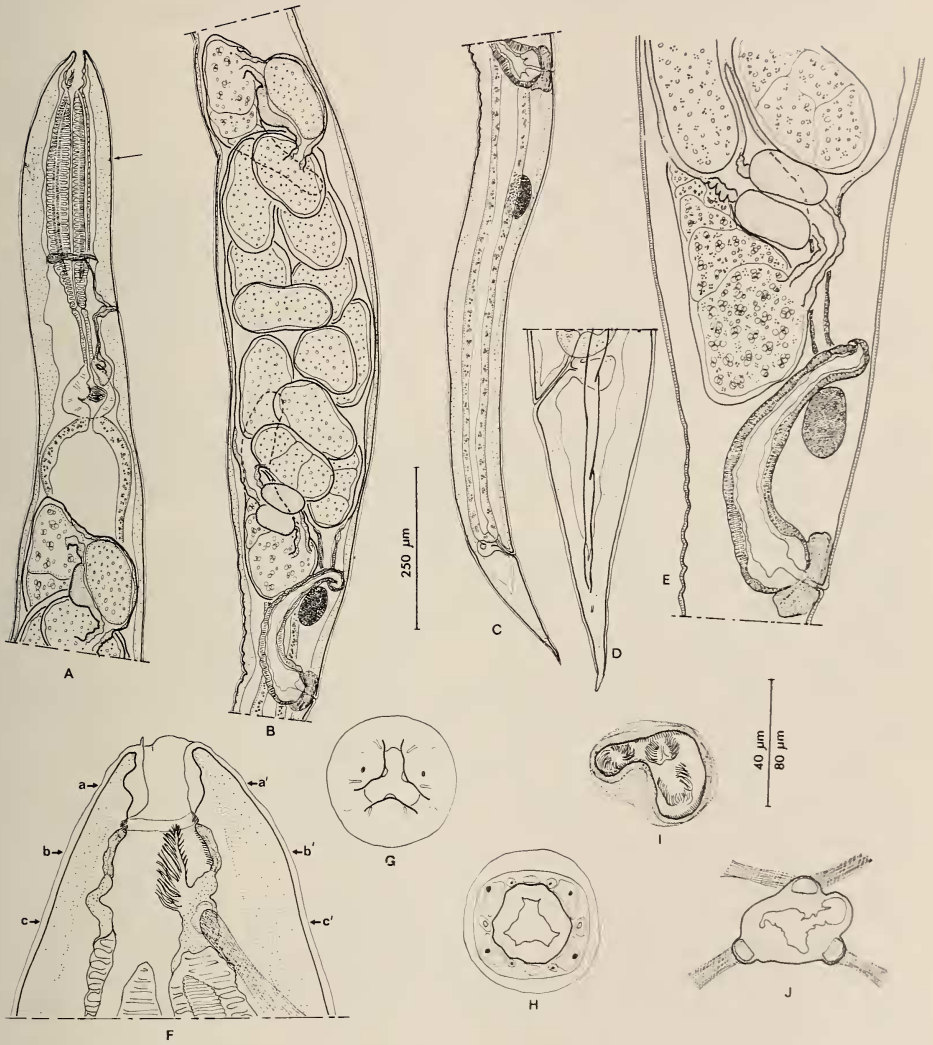


FIG. 7.

Ransomnema paraguayense n. sp., female. A, B and C, lateral view of entire worm in three segments; note hemizonid (arrow in A). D, caudal extremity, lateral view. E, vulva and vagina, lateral view. F, optical section through buccal capsule, lateral view. G, superficial apical view. H, I and J, optical sections through buccal capsule at levels a/a', b/b' and c/c' respectively of F.

(A to C = 250 µm scale; D, E = 80 µm scale; F to J = 40 µm scale)

***Carnoya mackintoshae* n. sp.**

Material Examined: One male and two females were recovered from KP 159, and three males (including holotype) and two females were found in KP 160 (also MHNG 982.1731).

DESCRIPTION (Figs 8 and 9)

General: Relatively small worms with narrow, flattened cephalic extremities and long conical to attenuate caudal extremities. Lips and lateral alae absent.

Male: Body cuticle with distinct transverse striations beginning just posterior to cephalic extremity, about 6 μm in cervical region and about 4 μm apart near midbody. Oral opening subtriangular, surrounded by four large outer cephalic papillae and two amphids; inner papillae arranged as one dorsal and two subventral pairs, each pair forming oval swelling just inside oral opening.

Buccal cavity consisting of: (1) short anterior portion lined by cuticle apparently continuous with body cuticle; (2) long middle portion, subtriangular in apical view, its lining formed by series of cuticular rings, therefore appearing striated in lateral view; (3) broad portion, roughly circular in apical view and with one dorsal and two subventral delicate cuticular projections at its base.

Oesophageal corpus spindle-shaped, abruptly becoming broader just posterior to nerve ring. Testis reflexed about 350 μm posterior to base of oesophagus, leading to seminal vesicle filled with spherical spermatids; spermatids in midregion of seminal vesicle commonly closely associated with small amber-colored globules. Seminal vesicle separated from swollen *vas deferens* by narrow tube.

Spicules robust, closely adpressed, invested by cuticular membrane and commonly twisted in everted position. Gubernaculum boat-shaped with ventral keel running between spicules, and with lateral flanges holding spicules together.

Thirteen caudal papillae: one pair subventral about 110 μm anterior to anus; one pair just anterior to anus, slightly more lateral; transverse row of three papillae on anterior anal lip; three subventral postanal pairs, most anterior pair about 140 μm from anus. Phasmids located at about same level as last pair of caudal papillae.

Caudal musculature consisting of series of oblique muscles beginning just behind anterior extremity of testis and continuing to near level of phasmids on either side of body.

Anus surrounded by cuticular ring thickest posteriorly and controlled by three pairs of muscles: one oriented anteriolaterally attached to anterior portion of ring, one oriented laterally attached to lateral portion and one oriented posterolaterally attached to posterior portion.

Female: Transverse markings on body cuticle arranged as follows: first about 6 μm from anterior extremity; second to fourth defining striae 1.3 to 1.6 μm wide; fifth to seventh defining annules about 6 μm wide; subsequent markings defining annules about 7 μm wide in oesophageal region and about 5 μm wide near midbody.

Seventeen to twenty-three transverse rows of spines present, beginning at level of seventh annule, continuing posteriorly on every second annule and ending near level of posterior extremity of oesophageal corpus. Spines in anterior 8 rows commonly terminating in multiple points; first twelve rows with 20 to 25 spines and subsequent rows with 10 to 16 spines. Occasional isolated spines present posterior to level of oesophageal corpus.

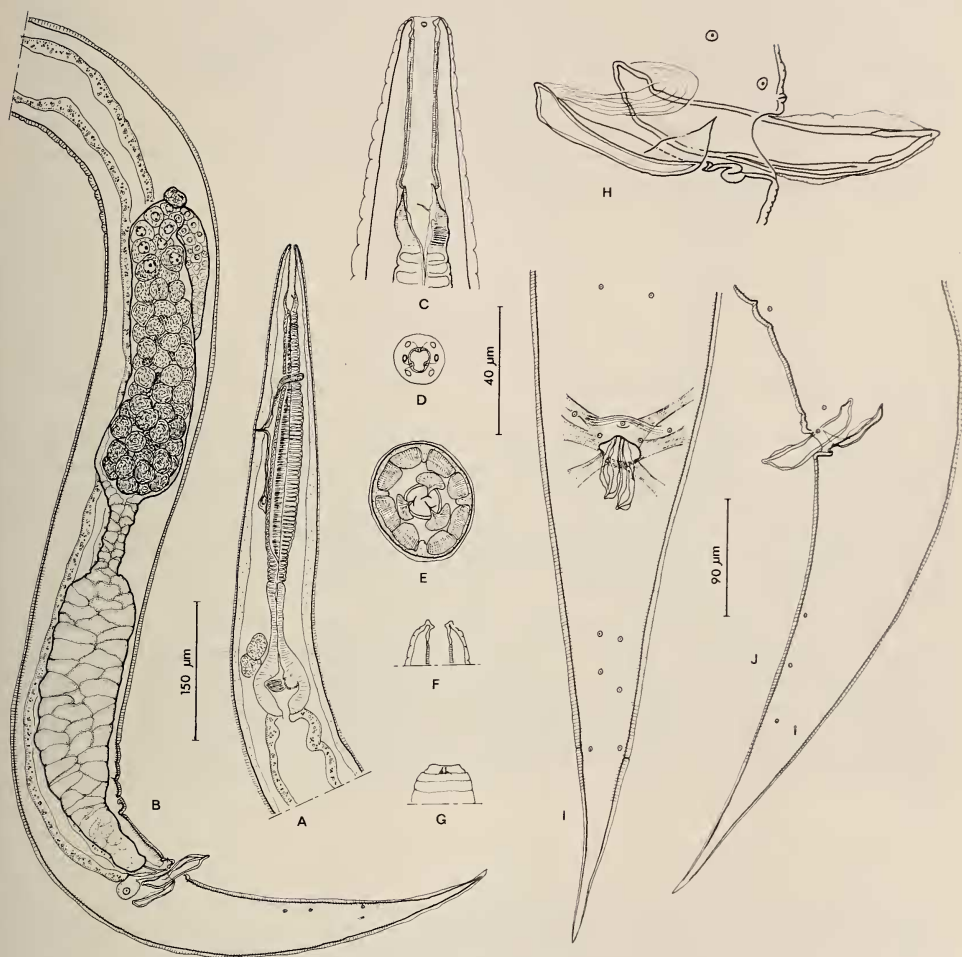


FIG. 8.

Carnoya mackintoshae n. sp., male. A and B, anterior and posterior halves of worm. C to G, cephalic extremity; C, lateral view, optical section through buccal capsule; D, superficial apical view; E, apical view, optical section through base of buccal capsule; F and G, detail of anterior extremity in optical section and superficial view showing transverse markings on cuticle. H, spicules and gubernaculum, lateral view. I and J, caudal extremity, ventral and lateral views.

(A, B = 150 μ m scale; C to H = 40 μ m scale; I, J = 90 μ m scale)

Oral opening surrounded by many small irregular lobes. Cephalic sense organs consisting of four submedian pairs of outer papillae (more median element in each pair smaller than more lateral element), two smaller lateral papillae and two amphids.

Anterior extremity of buccal capsule formed by one dorsal and two subventral plates, V-shaped in apical view, arranged around hexagonal lumen. One dorsal and two subventral tooth-like formations present projecting into anterior extremity of buccal cavity. Buccal cavity subtriangular in apical view just anterior to oesophagus. Lumen of narrow anterior portion of corpus hexagonal and lined by striated cuticle.

Vulva near midbody, non-salient. Opening to vagina highly undulated in ventral view. Reproductive system monodelphic and digonant.

DIMENSIONS

M a l e (mean and standard deviation of 4 specimens, of which holotype in parentheses).

Length 2.26 ± 0.13 (2.34) mm. Maximum width 159 ± 14 (147) μm near midbody. Buccal cavity 83 ± 7 (83) μm long of which posterior 23 ± 2 (23) μm surrounded by oesophageal tissue. Corpus 333 ± 21 (337) μm and isthmus 89 ± 4 (92) μm long. Bulb 76 ± 5 (73) μm long and 74 ± 8 (68) μm wide. Nerve ring 153 ± 6 (160) μm , excretory pore 232 ± 18 (252) μm and flexure of testis 957 ± 94 (1061) μm from anterior extremity. Spicules 96 ± 11 (91) μm , gubernaculum 59 ± 3 (60) μm and tail 393 ± 12 (408) μm long.

F e m a l e (mean and standard deviation of four specimens). — Length 2.65 ± 0.17 mm. Maximum width 224 ± 56 μm near midbody. Buccal cavity 14 ± 1 μm and anterior portion of corpus 83 ± 3 μm long. Posterior portion of corpus 159 ± 11 μm long and 66 ± 5 μm wide. Isthmus 148 ± 4 μm long. Bulb 105 ± 3 μm long and 104 ± 10 μm wide. Nerve ring 86 ± 2 μm , excretory pore 172 ± 17 μm and vulva 1.06 ± 0.04 mm from anterior extremity. Tail 688 ± 95 μm long. Eggs 161 ± 9 μm long and 84 ± 7 μm wide.

DISCUSSION

This species resembles *C. dollfusi* Adamson, 1984 in several respects: lateral alae are absent; there are no lips nor cervical spines in males; the first pair of postanal papillae are more than 100 μm from the anus; the excretory pore of the female is on a short conical projection.

The two species differ principally on the basis of female morphology: there are fewer spine rows in the new species (17-23 as compared with 25-30 in *C. dollfusi*); cephalic papillae are terminal in *C. dollfusi* but are subterminal in the present material; three teeth (one dorsal and two subventral) are present at the base of the buccal cavity in *C. dollfusi* but are absent in the new species; the opening to the vagina is thrown into 16 undulations in the new species but only 8 to 10 in *C. dollfusi*.

Males of the two species differ in spicule structure: the spicules are more robust and are invested by a cuticular membrane in *C. mackintoshae*.

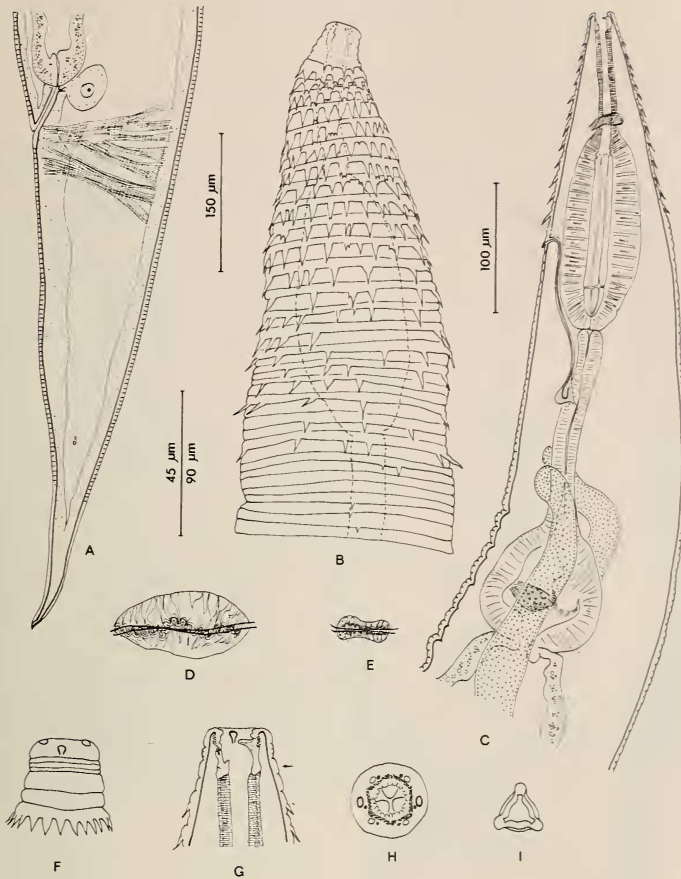


FIG. 9.

Carnoya mackintoshae n. sp., female, except for E. A, caudal end, lateral view. B, anterior extremity showing cuticular ornamentation. C, oesophageal region, lateral view. D, vulva, ventral view. E, vulva of *Carnoya dollfusi* paratype, ventral view. F, cephalic extremity, superficial lateral view. G, optical section through buccal capsule, lateral view. H, superficial apical view. I, optical section through buccal capsule at level indicated by arrow in G, apical view.

(A = 150 µm scale; B = 90 µm scale; C to E = 100 µm scale; F to I = 45 µm scale)

***Rhigonema subulata* (Artigas, 1926)**

Material Examined: Seventy-two males, 83 females and 39 larvae were collected from KP 159 and 44 males, 61 females and 60 larvae were collected from KP 160 (also 982.1732).

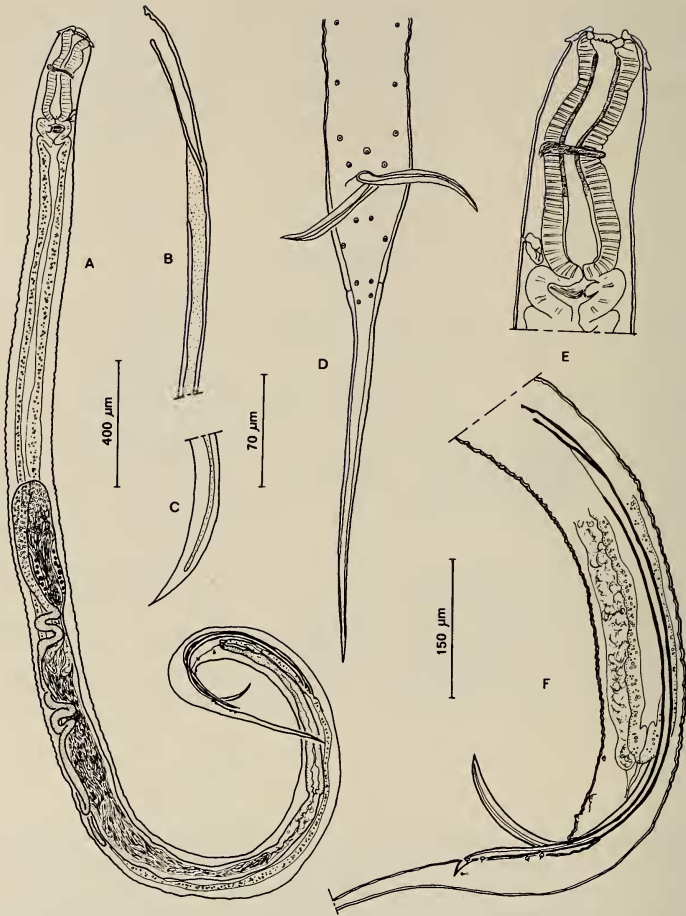


FIG. 10.

Rhigonema subulata (Artigas, 1926), male. A, entire worm, lateral view. B and C, proximal and distal extremities of spicule. D, caudal extremity, ventral view. E, oesophageal region, lateral view. F, caudal extremity, lateral view.

(A = 400 μm scale; B, C = 70 μm scale; D to F = 150 μm scale)

DESCRIPTION (Figs 10 and 11)

General: Long slender worms with attenuate caudal extremities. Cuticular spines absent. Body cuticle with fine striations about $1\ \mu\text{m}$ apart ending near level of phas-mids.

Cephalic extremity with cephalic cap and posterior collar separated from cap by groove. Oral opening subtriangular, surrounded by one dorsal and two subventral fleshy lobes. Four large submedian outer and six small inner papillae present. Amphids in groove between cephalic cap and collar.

Cuticle lining anterior extremity of oesophagus forming jaw apparatus consisting of one dorsal and two subventral V-shaped pieces with tooth-like formations on their luminal surfaces. Oesophageal corpus long and slender, its intimal lining with six longitudinal rod-like thickenings striated in side view. Bulb wider than long.

Male: Testis, its blind end posterior to midbody, undulating anteriorly and flexing posteriorly before meiosis zone. Spermatids elongate; epithelium in meiosis zone containing amber coloured granules. Meiosis zone separated from seminal vesicle by constriction; opening into seminal vesicle by way of short antechamber. Vas deferens long and slender.

Spicules similar, arcuate, long and slender with sharply pointed distal extremities. Seventeen caudal papillae present: four pairs subventral pre-anal; one unpaired on anterior anal lip; four pairs subventral postanal of which second pair slightly more lateral. Phas-mids between second and last papilla pair.

Female: Prominent prevulvar and less prominent postvulvar swellings present. Reproductive system amphidelphic and reflexed. Muscular vagina running anteriorly, becoming narrower and dividing into anterior and posterior uterine branches containing eggs arranged in single file. Uteri leading to oval seminal receptacles and through oviducts to ovaries. Flexure of anterior branch of reproductive system near level of second last oocyte; that of posterior branch at level of oviduct.

DIMENSIONS

Male (mean and standard deviation of 4 specimens). — Length 4.27 ± 0.51 mm. Maximum width $152 \pm 7\ \mu\text{m}$ near midbody. Buccal cavity $15 \pm 2\ \mu\text{m}$ and oesophagus $351 \pm 19\ \mu\text{m}$ long; the latter consisting of corpus $301 \pm 18\ \mu\text{m}$ long and bulb $69 \pm 5\ \mu\text{m}$ long and $115 \pm 5\ \mu\text{m}$ wide. Nerve ring $158 \pm 13\ \mu\text{m}$, excretory pore $269 \pm 22\ \mu\text{m}$ and anterior flexure of testis 1.31 ± 0.20 mm from anterior extremity. Spicules $792 \pm 46\ \mu\text{m}$ and tail $541 \pm 39\ \mu\text{m}$ long.

Female (mean and standard deviation of 6 specimens). — Length 4.75 ± 0.34 mm. Maximum width $163 \pm 11\ \mu\text{m}$ near midbody. Buccal cavity $12 \pm 2\ \mu\text{m}$ and oesophagus $339 \pm 20\ \mu\text{m}$ long; latter consisting of corpus $289 \pm 15\ \mu\text{m}$ long and bulb $61 \pm 5\ \mu\text{m}$ long and $108 \pm 6\ \mu\text{m}$ wide. Nerve ring $151 \pm 5\ \mu\text{m}$, excretory pore $262 \pm 17\ \mu\text{m}$, flexure of anterior branch of reproductive system $980 \pm 73\ \mu\text{m}$, vulva 2.28 ± 0.21 mm and flexure of posterior branch of reproductive system 2.86 ± 0.21 mm from anterior extremity. Tail $771 \pm 59\ \mu\text{m}$ long, and eggs $69 \pm 3\ \mu\text{m}$ wide and $89 \pm 2\ \mu\text{m}$ long.

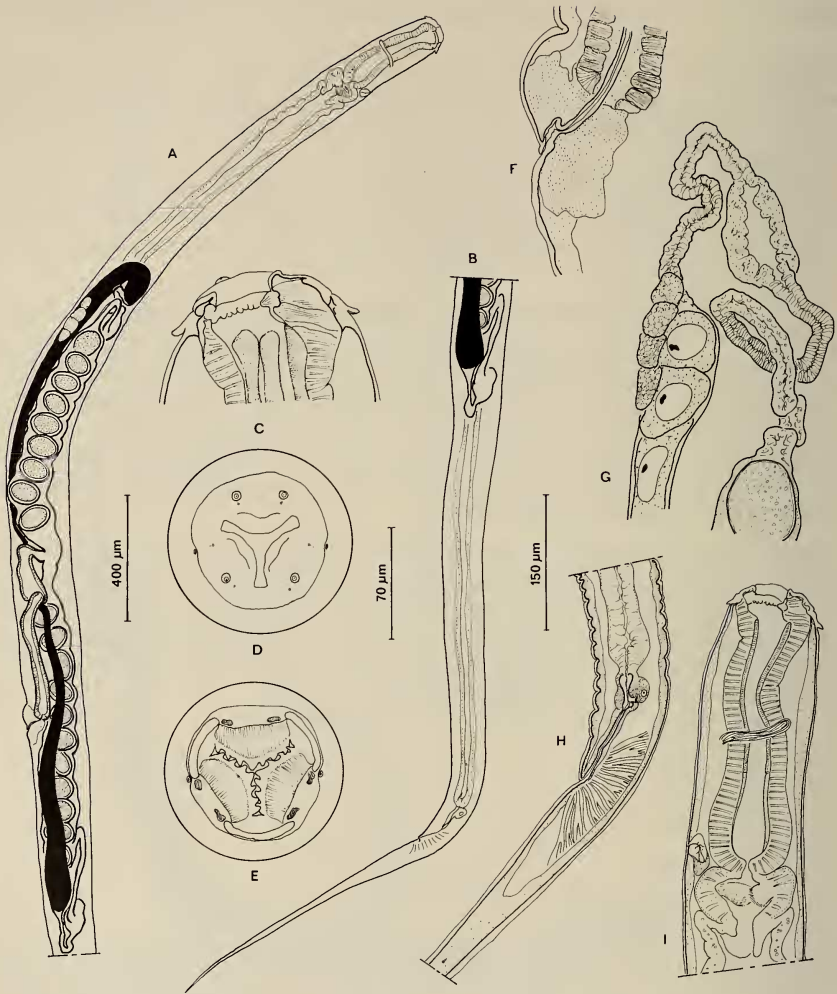


FIG. 11.

Rhigonema subulata (Artigas, 1926), continued. A and B, female, entire worm in two segments. C to E, cephalic extremity, male: C, optical section through buccal capsule and anterior end of oesophagus, lateral view; D, superficial apical view; E, optical section at level of jaw apparatus, apical view. F, vulvar region, lateral view. G, junctions of anterior ovary, oviduct and uterus showing coelomocytes, dissection. H, anal region, lateral view.

(A, B = 400 μ m scale; C to F = 70 μ m scale; G to I = 150 μ m scale)

DISCUSSION

Rhigonema subulata was originally described from an unidentified diplopods from Manguinhos (Federal District) and from Rio de Janeiro and Sao Paulo, Brazil. ARTIGAS described the male but was unable to distinguish females from those of *R. falcatum* (Artigas, 1926).

The present material agrees very closely with Artigas' description and illustrations in spicule size and shape, and in disposition of caudal papillae. I therefore assign it to *R. subulata*. A complete description of the material is given since I was not able to compare it with Artigas' types. These apparently no longer exist (TRAVASSOS & KLOSS 1960).

NEMATODE PARASITES OF DIPLOPODS AND R- AND K-SELECTION

Rhinocricus bernardinensis in Paraguay is parasitized by seven nematode species; all inhabit the posterior intestine. In addition to the six described here, *Thelastoma dessetae* (Oxyurida) was described from the same host individuals in a previous study (ADAMSON 1985). This fauna is similar to that observed in many Spirostreptida and Spirobolida (Diplopoda) and consists of three superfamilies, namely the Thelastomatoidea (Oxyurida), the Rhigonematoidea and the Ransomnematodea (Rhigonematida) (see for example KLOSS 1961).

Species flocks of parasitic nematodes, like those of free-living organisms, generally consist of closely related species (CHABAUD 1956; DURETTE-DESSET 1971; INGLIS 1965, 1971; CHABAUD & DURETTE-DESSET 1978). DURETTE-DESSET (1971) and INGLIS (1971) hypothesized that such faunae result from successive allopatric speciations beginning with a single parent species. The nematode fauna of diplopods is thus exceptional since it is composed of descendants of three parasitic lineages. A similar, though less dramatic situation occurs in tortoises which harbour attractid (Ascaridida) and pharyngodonid (Oxyurida) parasites in their colon (PETTER 1966).

CHABAUD & DURETTE-DESSET (1978) recognized two types of species flocks of parasitic nematodes, namely those which are rich and stable in terms of numbers and relative abundance of species, and those which are less rich and unstable. The authors concluded that the two faunal types correspond to two types of environment: one in monophagous hosts which favours K-selection (harbouring a rich, stable fauna) and one in polyphagous hosts which favours r-selection (harbouring a more impoverished, unstable fauna). The essential difference between r-selected and K-selected species lies in the proportion of energy devoted to reproduction. Parasitism is a life-history tactic which tends to result in r-selection since the fundamental problem of parasites is one of colonization; only a few of the infective stages produced actually reach a suitable host. However, the nematode fauna of diplopods appears to be a mixture of more or less K-selected and more or less r-selected species.

The Rhigonematoidea are the most K-selected of the diplopod parasites. They are large and probably long-lived, and some reports suggest they attach to the intestinal mucosa (LEIDY 1853; CLARK 1978). We could expect population levels in K-selected species to be stable at or near the carrying capacity, and competition is therefore severe. This is consistent with the fact that rhigonematids, although often numerous, are generally

TABLE 1

Intensities (number of worms per host) of nematode parasites in two specimens (KP159 and KP160) of *Rhinocricus bernardinensis* (Diplopoda) from Paraguay.

PARASITE	ADULTS KP159:KP160	LARVAE KP159:KP160	TOTAL KP159:KP160
Rhigonematoidea			
<i>Rhigonema subulata</i>	155:105	39:60	194:165
Ransomnematoida			
<i>Heth clunyi</i>	5:1	0:0	5:1
<i>H. parartigasi</i> ¹	8:2	0:0	8:2
<i>H. magnavulvaris</i> ¹	19:5	0:0	19:5
<i>Heth</i> sp. ²	20:4	0:0	20:4
<i>Ransomnema paraguayense</i>	3:2	1:2	4:4
<i>Carnoya mackintoshae</i>	3:5	0:0	3:5
Thelastomatoidea			
<i>Thelastoma dessetae</i> ³	1:2	0:0	1:2

¹ females only

² males of *H. parartigasi* and/or *H. magnavulvaris*.

³ data from ADAMSON 1985.

represented by only one or two species in a given host. In the present study *R. subulata* was the only rhigonematid recovered and it dominated the nematode fauna numerically as well as in terms of biomass (Table 1).

The Ransomnematoida and probably also the Thelastomatoidea are more r-selected. They are small and therefore probably short-lived, and live unattached in the intestinal lumen. Population levels of r-selected forms tend to be variable but usually well below carrying capacity, and competition is therefore often lax. Ransomnematoids and thelastomatoids are often represented by several species. In the present study five ransomnematoids were found and, although only one thelastomatoid was found, the superfamily is more richly represented in other diplopod hosts (cf. KLOSS 1961); intensities were extremely low.

Curiously, although they are r-strategists, most ransomnematoids produce relatively small numbers of large eggs, a characteristic generally associated with K-strategists. The innate capacity for increase, 'r', may be increased by increasing fecundity and/or by decreasing generation time; ransomnematoids have apparently opted for the latter strategy. Their small size probably implies a short generation time. However, it also limits the number of eggs females can produce and this necessitates a higher investment per egg (indicated by their relatively large size) on the part of the female.

RÉSUMÉ

Six Rhigonematides (Rhigonematida; Nematoda), dont cinq nouvelles espèces sont décrits chez *Rhinocricus bernardinensis* (Rhinocricidae; Spriobolida; Diplopoda) récoltés

dans la région des chutes d'Iguassu pendant une expédition zoologique au Paraguay. *Heth clunyi* n. sp. est proche de *H. spinosum* mais en diffère légèrement par l'ornementation cuticulaire cervicale de la femelle, et par un spicule plus grand dont l'extrémité est bifide. *Heth parartigasi* n. sp. et *H. magnavulvaris* n. sp. sont proches de *H. artigasi*. Les trois espèces se distinguent par la morphologie vulvaire et prévulvaire de la femelle: chez *H. parartigasi* la vulve n'est pas salliante et il y a une *area rugosa*; chez *H. magnavulvaris* et *H. artigasi* la vulve est salliante et l'*area rugosa* est absente; chez *H. artigasi* la lèvre antérieure de la vulve surplombe légèrement la lèvre postérieure tandis que chez *H. magnavulvaris* la lèvre antérieure forme un gros lobule en surplomb. Des mâles correspondants soit à *H. parartigasi* soit à *H. magnavulvaris* sont décrits comme *Heth* sp. et diffèrent de ceux de *H. artigasi* par un gubernaculum et un spicule plus longs, et par l'extrémité bifide du spicule. *Ransomnema paraguayense* n. sp. est proche de *R. christiei* mais en diffère par la disposition des papilles caudales et par son spicule plus long. *Carnoya mackintoshae* n. sp. est proche de *C. dollfusi*. Les femelles des deux espèces diffèrent par l'ornementation cuticulaire cervicale, par la position des papilles cervicales, subterminale chez *C. mackintoshae* et terminale chez *H. dollfusi*, par l'absence de dents à la base de la cavité buccale chez la nouvelle espèce, et par la forme de la vulve; les mâles diffèrent légèrement par la forme du spicule. *Rhigonema subulata* (Artigas, 1926) est redécrite.

La faune de Nématodes parasites de l'intestin postérieur des diplopoques diffère des autres exemples ou plusieurs parasites coexistent dans le même organe d'un hôte parce qu'elle est constituée par trois superfamilles (Thelastomatoidea, Rhigonematoidea et Ransomnematoida) et non pas par une seule lignée. Il est suggéré que les Rhigonematoidea utilisent une stratégie-«K» tandis que les Ransomnematoida utilisent une stratégie plutôt «I».

BIBLIOGRAPHY

- ADAMSON, M. L. 1983. Redescriptions of five species of *Heth* Cobb, 1898 (Rhigonematidea; Nematoda) from South America. *Syst. Parasitol.* 5: 185-202.
- 1984. A revision of the genus *Carnoya* Gilson, 1898 (Nematoda; Rhigonematidae) with descriptions of four new species. *Syst. Parasitol.* 6: 113-129.
- 1985. *Thelastoma dessetae* n. sp. (Thelastomatoidea; Oxyurida; Nematoda) from Paraguayan diplopods with comments on reproductive anatomy in *Thelastoma*. *Revue suisse Zool.* 92: 413-420.
- ARTIGAS, P. 1926. Nematoides de Invertebrados (IV). *Bolm biol. Lab. Parasit. Fac. Med. S. Paulo* 1: 97-110.
- 1929. Systematica dos Nematoides dos Arthropodes. *Thesis, Faculdade de Medicina S. Paulo.* 113 pp.
- CHABAUD, A. G. 1956. Remarques sur les Nématodes parasites du caecum des Eléphants, milieu très préservé des phénomènes de sélection. *C. n. hebd. Séanc. Acad. Sci., Paris*, 243: 436-439.
- CHABAUD, A. G. and M. C. DURETTE-DESSET. 1978. Parasitisme par plusieurs espèces congénériques. *Bull. Soc. zool. Fr.* 103: 459-463.
- CLARK, W. C. 1978. New species of rhigonematid and thelastomatid nematodes from the pill millipede *Procyliosoma tuberculata* (Diplopoda; Oniscomorpha). *N. Z. J. Zool.* 5: 1-6.

- DOLLFUS, R. P. 1952. Quelques Oxyuroidea de Myriapodes. *Anns Parasitol. hum. comp.* 27: 143-236.
- DURETTE-DESSET, M. C. 1971. Essai de classification des Nématodes Héligmosomes. Corrélation avec la paléobiogéographie des hôtes. *Mem. Mus. natn Hist. nat., Paris, Nelle Sér., Sér. A. Zool.* 69: 1-126.
- INGLIS, W. G. 1965. Patterns of evolution in parasitic nematodes. *In Evolution of Parasites. Third Symposium of the British Society for Parasitology. Blackwell Scient. Publ., Oxford.*, pp. 79-124.
- 1971. Speciation in parasitic nematodes. *Adv. Parsitol.* 9: 185-223.
- KLOSS, G. R. 1961. Parasitos intestinais do Diplopoda *Scaphiostreptus buffalus* Schubart. *Bolm Mus. para. Emilio Goedli, Nov. Ser., Brasil, Zoologia* 35: IV+13 pp.
- LEIDY, J. 1853. A flora and fauna within living animals. *Smithson. Contr. Knowl.* 5:X+67 pp.
- PETTER, A. J. 1966. Equilibre des espèces dans les populations de Nématodes parasites du colon des Tortues terrestres. *Mém. Mus. nat. Hist. nat., Paris, Nelle Sér., Sér. A. Zool.* 39: 1-252.
- TRAVASSOS, L. and G. R. KLOSS. 1960. Compendio dos Nematoides parasitos intestinais de Artropodos. I. Cephalobiidae, Robertiidae e Rhigonematidae. *Archos Mus. nac., Rio de J.* 50: 237-303.